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A COMPARATIVE STUDY OF THE STRUCTURE OF THE PHOTOGENIC ORGANS OF CERTAIN AMERICAN LAMPYRIDÆ

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OF the great amount of work that has been done in the production of light by living forms, not a little has been devoted to the structure of the photogenic organs. The organs whose anatomy and histology have been the subject of most of the researches have been those of the Lampyridæ. Although perhaps twenty-five species of these widely distributed insects occur within the borders of the United States proper, but little work has been done on the anatomy and histology of their luminous organs. The late Dr. Wm. H. Seaman (1) made some observations on *Photinus pyralis*, the insect which is so common in the parks in Washington in the summer, and a near relative of the *pyralis*, *Photinus marginellus*, has been made the subject of an extensive study by Miss Townsend, at Cornell (2). Wielowiejski (4) mentions having studied two American species, but fails to give their names. With these exceptions, however, the American Lampyridæ seem to have been neglected in the matter of histologic studies of the photogenic organs. Of the foreign Lampyridæ which have been studied, the principal species are *Lampyris noctiluca*, *Phausis splendidula*, *Phosphænus hemipterus* and *Luciola italica*, all European species, and all belonging to different subgroups from each other and from the American insects. Many studies have also been made upon the cucuyo, *Pyrophorus noctilucus* Linn., the large tropical elaterid firefly.

It has been thought worth while, therefore, to attempt some further study of the photogenic organs of such species of Lampyridæ as are accessible here, having in view especially the determination of the similarities and differences between them and between them and other

species which had been studied previously. The two species most common here (Washington, D. C.) are *Photinus pyralis* Linn. and *Photuris pennsylvanica* Deg., and the majority of our studies have been made on them. The classification relationships between these insects and the others that have been studied may be seen from Oliver's recent catalogue (3). As already stated, *Photinus pyralis* had been studied to some extent by Seaman, and its near relative, *P. marginellus*, by Townsend, but so far as we have been able to find, no studies have been made on any species of *Photuris*.¹

A large number of slides have been made, containing transverse, longitudinal and oblique sections of the two insects above mentioned, and a few transverse sections of *Photinus consanguineus*. With these slides comparative studies of the structure of the photogenic organs have been made. The most essential result of these studies is that in these three species the structure of the photogenic organs is practically identical, and very similar to that described for some of the other species of Lampyridæ which have been examined. Many of the drawings given by Townsend of the structures in *Photinus marginellus* may represent with equal faithfulness the corresponding structures in *Photinus pyralis* and *Photuris pennsylvanica*; our slides of *Photinus consanguineus* were not entirely satisfactory, but so far as could be seen, the structures in this insect are identical with those in its larger congener, *pyralis*.

In all three insects the luminous organ is divided into two distinct layers, the inner one being white and opaque, and serving as a reflector, and the outer being yellowish and translucent, and containing the actual photogenic mechanism. The photogenic organs, as brought out by prior studies, are penetrated from the interior of the insect outward, by innumerable tracheæ, which ramify and anastomose within the true photogenic tissue, and unite within, above the reflecting layer, to

¹ Since this was written, it has been noted that Watasé (9) made a few observations on the structures in *Photuris pennsylvanica*, but makes only a brief reference to them.

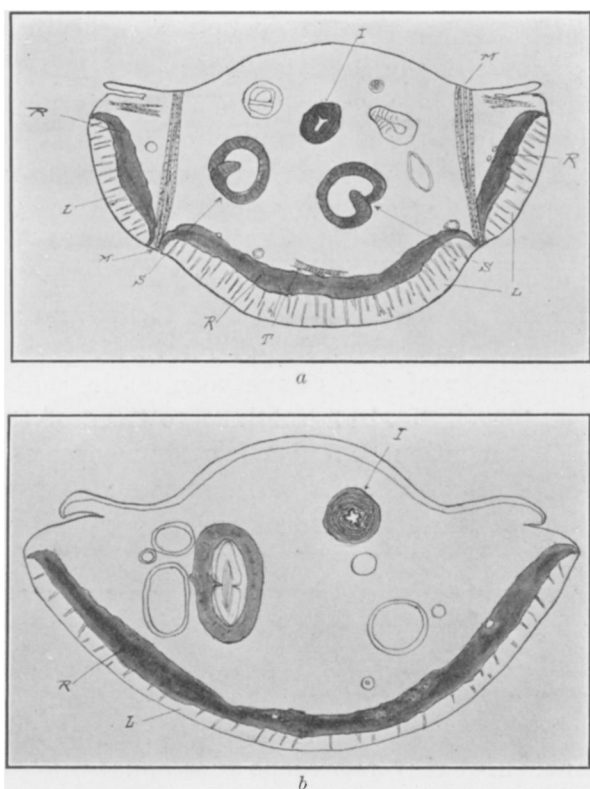


FIG. 1. Cross-sections at about the middle of the fifth abdominal segment of (a) *Photinus pyralis* and (b) *Photuris pennsylvanica*. I, intestine; L, photogenic tissue; M, muscle fibers; R, reflecting layer; S, spiral organs; T, tracheæ to photogenic organ.

form larger tracheæ; the latter lie nearly flat against the inside surface of this reflecting layer, and run diagonally outward, finally uniting almost at the spiracle with the breathing tracheæ, with which they are identical in appearance. The spiracles are on the dorsal side of the abdomen, one near either edge of each segment, and are furnished with some valvular arrangement at their orifice; the details of this structure have not yet been clearly made out. The arrangement of the smaller tracheæ and tracheoles is much the same in all three species. The tracheæ pass through the reflecting layer and the photogenic tissue perpendicularly to the surface. These tracheæ are furnished with chitinous hairs on the

interior as far as the point where they enter the reflecting layer; the presence of these hairs in tracheæ beyond this point and in the fine tracheoles, has not been observed. In their passage through the photogenic tissue, the tracheæ are surrounded by the structure referred to by Miss Townsend as the cylinder, a cylindrical mass of cells, sharply differentiated from those of the surround-

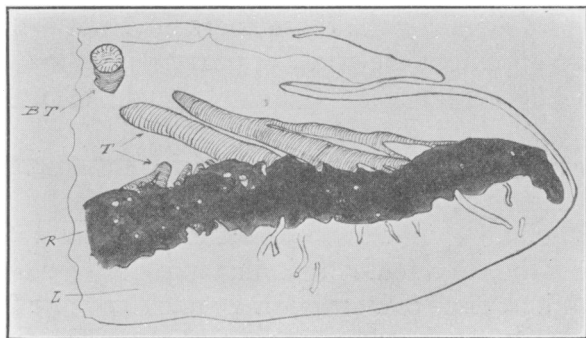


FIG. 2. Oblique section near edge of *Photinus pyralis*. *L*, photogenic tissue; *R*, reflecting layer; *T*, trachea to photogenic organ; *BT*, trachea leading to other organs. (Both of these figures are intended only as outline drawings, and no attempt has been made to show all the internal organs, or any great number of tracheæ.)

ing tissue, through which the trachea passes almost centrally. Within this cylinder the trachea throws off the numerous small branches, which at the edge of the cylinder break into the very fine tracheoles which pass into the photogenic tissue and anastomose between the cells with tracheoles from adjoining cylinders. The appearance of the large tracheæ above the luminous organ are shown in Fig. 2, drawn from an oblique section, the line of the cut being nearly parallel to the line of the larger tracheæ near the edge of the abdomen. At the lower end, just next to the superficial chitin covering the luminous segments, the main trachea subdivide into the large number of branches whose tracheoles radiate into the photogenic tissue, usually recurving slightly, so as to penetrate the tissue a short distance from the chitin.

The entire system suggests that the air is drawn in through the breathing tracheæ, and forced through the

fine passages in the true photogenic tissue, where the oxygen of the air is consumed in a biologic oxidation. In the sections of *pyralis* there are clearly seen bundles of muscle fibers on either side of the center line of the insect, which pass completely through the abdomen, almost vertically, and are attached to the exterior chitin at the top and bottom. At about the same point, other muscle fibers pass inward from the point of maximum width at each side; these fibers have not been traced to their full extent, but they appear to pass upward and toward the center near the dorsal side of the insect. These fibers are indicated in Fig. 1, *a*, at *M*. No similar muscle fibers have been observed in *Photuris*, although short lengths of muscle fiber passing vertically through the abdominal cavity have occasionally been noted, and these may be fragments of similar muscles to those in the Photinini. The corresponding muscles of *Photinus marginellus* are clearly shown in Fig. 1 of Miss Townsend's paper. Externally, the lower terminations of these bundles of muscle fibers appear as non-photogenic spots on the ventral surface of the luminous segments.

It may be well here to call attention to certain differences between *Photuris* and *Photinus*, as shown by the cross-sections of the insects. While there is a general similarity of outline in the cross-sections of the two species, the section of *Photuris* is generally a little flatter, and the ventral curvature of a somewhat larger mean radius, than in *Photinus*. Another difference has been very marked in our sections. While the thickness of the reflecting layer is about the same in both species, the layer of true photogenic tissue is much thinner, both actually and in comparison with the reflecting layer, in *Photuris* than in *Photinus*; this difference is clearly seen by reference to Fig. 1, *a* and *b*. This difference may be somewhat significant when considered in connection with the slight differences in the quality of the emitted light, and in the modes of emission of the two species. (See reference No. 8.) In *Photinus* there are two peculiar organs each consisting apparently of a thick-walled,

chitinous tube, coiled into a nearly cylindrical spiral, represented in partial section by *S, S*, in Fig. 1, *a*; these two organs appear to be glands which empty into a common duct which could be followed to the posterior extremity, and it seems possible that they are a portion of the male generative system, as they were not found in the female *pyralis*, although no spermatozoids were seen. The direction of rotation of the spiral was the reverse on the left side of the insect from that on the right. These organs were not found in the *Photuris*, although globular, glandular structures were found in approximately the same portion of the latter insect. This structure is shown in Fig. 2 of Miss Townsend's paper on *Photinus marginellus*, and in Fig. 1 of Seaman's (*Photinus pyralis*); the latter erroneously referred to it as the intestine; in our studies, the intestine of both *Photinus* and *Photuris* was seen as a nearly straight, thick-walled tube, indicated in section by *I* in *a* and *b* of Fig. 1.

The above remarks apply to the male insects. The two sexes in *Photuris* are almost indistinguishable externally; all those which we sectioned appeared to be males. In *Photinus pyralis*, however, the female differs markedly from the male. The luminous organ in the male occupies the entire ventral surface of the fifth and sixth segments of the abdomen, and the posterior portion of the fourth segment. In the female, the luminous apparatus is visible externally as a small, rectangular yellow spot, occupying about one third of the ventral area of the fifth segment of the abdomen. This organ obtains its air supply from a large trachea which extends along its forward edge, and apparently connects with the spiracles on the dorsal edges of the segment. In its finer structure, the photogenic organ of the female *pyralis* appears to be exactly like that of the male, as is to be expected.

That the photogenic process is an oxidation is scarcely to be doubted, in view of the work which has been done already. The work of one of us (McD.) with Professor

Joseph H. Kastle, of the University of Virginia, is of especial interest in this connection (6).

Our histologic methods presented no particularly new features. Most of our specimens were killed in hot 70 per cent. alcohol, stained entire in acid carmine, and mounted in paraffin. To secure proper penetration of the stain, it was found necessary to clip off the tip of the abdomen, or to slit the dorsal chitin. Osmic acid preparations were used a number of times, and in the sections of *Photinus consanguineus*, which were otherwise unsatisfactory, one per cent. osmic acid gave very good results for the fine tracheolar structure. For the study of the tissues under the dissecting microscope a good treatment was found to be to allow the detached, fresh luminous segments to soak in a mixture of equal parts of ten per cent. caustic soda and ten per cent. formaldehyde solution for three or four hours. This treatment left the tissues of both the reflecting and the active layers of the same gross appearance, though without entirely destroying the cellular structure; after being treated thus, the tracheæ and tracheoles can be seen as silvery white tubes and threads, on a background of dull, pale yellow, and may be followed down to the point of anastomosis.

It seems possible that the reflecting layer fulfils a two-fold purpose—that of reflecting the light outward, and thus increasing its intensity in the desired direction, and of protecting the insect itself from its own radiations. It has recently been shown by Coblentz (7) that the *pyralis* and other Lampyridæ contain a fluorescent material, and a number of observers have shown that fluorescent materials injected into a living animal show a higher degree of toxicity when the animal subsequently is exposed to light than if it be left in the dark.

To conclude: We have found that (a) the structure of the photogenic organs in *Photinus pyralis*, *Photinus consanguineus* and *Photuris pennsylvanica* is practically the same, and very similar to the structures of the corresponding organs in some of the other species of Lampyridæ that have been studied; (b) the tracheæ from

the photogenic organs connect near the breathing spiracle with the tracheæ which supply the other organs, and that they closely resemble the latter tracheæ in structure; (c) the view that the photogenic process is an oxidation is borne out by the structure of the photogenic organs.

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No attempt will be made here to give a complete list of the references to the literature of even the histology of the luminous tissues; so far as the latter branch of the subject is concerned, it is pretty thoroughly covered by the bibliography given by Miss Townsend, and the most complete bibliography yet published of the whole subject of physiologic light is contained in Mangold's extensive and interesting review cited as reference No. 5, below.

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